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How Our Ancestors Broke through the Gray Ceiling

Comparative Evidence for Cooperative Breeding in Early *Homo*

by Karin Isler and Carel P. van Schaik

The "expensive brain" framework proposes that the costs of an increase in brain size can be met by any combination of increasing the total energy turnover or reducing energy allocation to other expensive functions, such as maintenance (digestion), locomotion, or production (growth and reproduction). Here, we explore its implications for human evolution. Using both comparative data on extant mammals and life-table simulations from wild extant apes, we show that primates with a hominoid lifestyle face a gray ceiling that limits their brain size, with larger values leading to demographic nonviability. We argue that cooperative care provides the most plausible exaptation for the increase in brain size in the *Homo* lineage.

For a change in any character to be adaptive, it must bring a net fitness benefit relative to the ancestral state. To explain the evolution of larger brains, many hypotheses have been devised that focus on the adaptive benefits without considering the costs (e.g., Dunbar 1998). Here, following the early proponents of an energetic viewpoint (e.g., Aiello and Wheeler 1995; Martin 1981), we argue that the high costs of brain tissue relative to those of other organs (Rolfe and Brown 1997) should also be considered because they may limit the net benefits to those situations where the survival benefits of larger brains outweigh the demographic consequences of the increased allocation of energy. Indeed, given that absolute brain size is tightly correlated with overall cognitive performance (Deaner et al. 2007; Reader, Hager, and Laland 2011), most lineages would be able to derive a great variety of cognitive benefits from larger brains (e.g., Shettleworth 2010), suggesting the possibility that the ability to overcome the costs may in fact be limiting and thus may explain most of the brain-size variation in homeothermic vertebrates.

The "expensive brain" framework notes that evolutionary increases in brain size can be paid for in two complementary but nonexclusive ways (fig. 1): (i) by increasing energy turnover or (ii) by reducing allocation to other targets, such as maintenance, locomotion, and production (Isler and van Schaik 2009*a*). This framework can be applied to hominin evolution. Early *Homo* is associated with the first increase in brain size among hominins outside the range of brain sizes found among great apes (Schoenemann 2006). This increase in brain size has no doubt brought various cognitive benefits, perhaps to do with tool use or cooperative hunting or other forms of cooperation. The question pursued here, however, is how the increasing encephalization could be afforded (Aiello and Key 2002; Aiello and Wells 2002; Leonard et al. 2003).

Thus, following the first pathway, a part of the brain-size increase in early *Homo* may be attributed to an increase in metabolic turnover. Supportive evidence comes from the finding that the positive correlation between basal metabolic rate (BMR) and brain size is most pronounced in primates (Isler and van Schaik 2006*b*). Although the BMRs of humans and chimpanzees are similar and near the value predicted from the Kleiber line for their respective body mass (Kleiber 1961), humans exhibit a higher percentage of body fat compared with most primates (reviewed in Wells 2006), and thus BMR relative to lean body mass is likely to be higher than in chimpanzees (Aiello and Wells 2002). In addition, there is growing evidence for a pronounced difference in daily energy expenditure between humans and great apes (Pontzer 2012; Pontzer et al. 2010).

Environmental conditions should affect the potential reaction space for stabilizing the energy throughput on a higher level. Increased metabolic turnover may only be possible in habitats that allow for a continuous food supply. Thus, when periods of unavoidable food scarcity recur, we expect most species to be forced to evolve smaller brains than their sister taxa in less seasonal environments. Indeed, we found that seasonality in food (and hence energy) intake is negatively correlated with brain size in strepsirrhine and catarrhine primates (van Woerden, van Schaik, and Isler 2010; van Woerden et al. 2012) as predicted by the expensive brain framework. Work on birds, however, had earlier suggested that habitat

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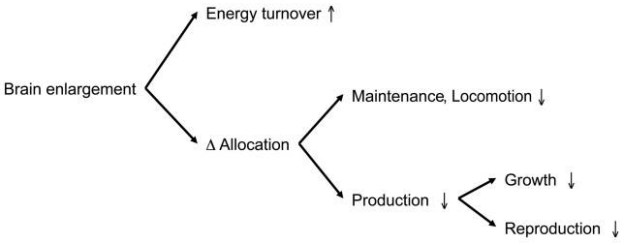

Figure 1. Expensive brain framework. From an ultimate perspective, any increase in brain tissue must be paid for either by any combination of increased energy turnover or by reduced energy allocation to other expensive body functions.

seasonality imposes selection on increased brain size (e.g., Sol 2009), a view known as the "cognitive buffer" hypothesis. This effect was also found among catarrhine primates in that relatively large-brained species show a larger difference between the seasonality of their habitat and the annual variation in food intake (van Woerden et al. 2012). Nevertheless, the relationship between relative brain size and habitat seasonality is neutral, indicating that the cognitive buffering may at best level out the energetic constraint (van Woerden et al. 2012).

The habitats invaded by early *Homo* were clearly more seasonal than the gallery forests, lacustrine edges, and woodlands inhabited by their ancestors (Potts 1998; Reed 1997). From the comparative evidence, we tentatively conclude that the increasing habitat seasonality was an important selective force in the early *Homo* lineage, although the primate data suggest that at this point it had not yet led to an increase in brain size. Rather, increasing habitat seasonality may have shaped the unique human combination of storing body fat in combination with cognitive solutions to survive irregular starvation periods (Navarrete, van Schaik, and Isler 2011; see also Kuzawa 1998; Wells 2010).

Turning to the second pathway, are there trade-offs between the brain and other expensive body functions that may explain early human encephalization? In a classic study, Leslie Aiello and coworkers proposed that energetic effects on human brain size were mainly linked to reduced allocation to intestinal tissues because of increased meat eating (Aiello and Key 2002; Aiello and Wheeler 1995). However, comparative support for this "expensive tissue" hypothesis is limited. Early studies had found no evidence for it in bats or birds (Isler and van Schaik 2006*a*; Jones and MacLarnon 2004). A recent study of a large sample of mammals, including 23 species of primates, with matching brain and organ mass data (Navarrete, van Schaik, and Isler 2011) also failed to support it. These results put the general validity of this hypothesis in doubt. Moreover, for the specific case of humans, we argue that the currently available data on great-ape digestive tract anatomy (Chivers and Hladik 1980) are not sufficiently clear to claim reduction of the gut in the human lineage (Hladik, Chivers, and Pasquet 1999).

Another trade-off, that between the energy used for locomotion and for the brain as shown in birds (Isler and van Schaik 2006*a*), may also have played a role in human evolution when in early *Homo* an energetically less efficient, australopithecine-like form of bipedalism evolved into a modern striding gait. The abandonment of the energetically very expensive climbing also freed these hominins from the anatomical compromise between climbing and walking (Isler and van Schaik 2006*a*). Apart from reducing costs of locomotion, this change in the locomotor habits may also have induced a reduction of maintenance costs during rest, as humans are reported to have relatively less muscle mass than great apes (Leonard et al. 2003; Snodgrass, Leonard, and Robertson 2009). However, this seeming difference could arise because of the higher amount of fat stores in humans. At present, hypotheses explaining increased encephalization in the human lineage with metabolic trade-offs through a shift in body composition are only weakly supported by empirical data (Muchlinski, Snodgrass, and Terranova 2012).

In this paper, we explore the trade-off between brain size and production, which includes growth and reproduction. This effect is well established among birds (e.g., Iwaniuk and Nelson 2003) and mammals (Isler and van Schaik 2009*a*, 2009*b*). Here, we will use correlations between life history characteristics and thus reproductive capacity and brain size in extant primates to shed light on the evolutionary history of early hominins. Briefly, we will argue that great apes have brain sizes that are close to the maximum achievable with their lifestyle and that our hominin ancestors could only break through this so-called gray ceiling after they had adopted cooperative breeding.

Table 1. Phylogenetic regressions of life history traits versus female brain and body mass data in nonhuman primates ($N = 86$ species)

		Female brain mass		Female body mass	
Life history parameter	λ	*P*	Effect	*P*	Effect
Neonate body mass	.959	<.0001	.674	.014	.209
Gestation	.996	.0005	.071	.095	−.084
Lactation	.737	<.0001	.811	.396	−.12
Interbirth interval	.925	.013	.461	.688	−.054
Litter size	.999	.017	−.242	.166	.097
Annual fertility	.955	.002	−.702	.355	.148
Age at first reproduction	.848	.0009	.573	.111	−.198
Maximum life span	.864	.0004	.425	.051	−.167
Maximum reproductive life span	.815	.001	.412	.064	−.171
r_{max}	.950	.0004	−.688	.172	.186

Source. Primate life history and female brain and body mass data are taken from the compilation described in van Schaik and Isler (2012).
Note. Phylogenetic least squares regressions were calculated with pglm.est in the R-package CAIC (Orme et al. 2010; Purvis and Rambaut 1995; R Development Core Team 2010). A λ value close to 1 indicates a strong phylogenetic influence on the respective parameters (Garland, Harvey, and Ives 1992).

Brain Size and Life History Traits: How Do Humans Differ?

From the expensive brain framework it follows that an increase in relative brain size could be paid for by reduced investment in production (i.e., slowing down growth, reducing reproduction, or both). We have shown that relatively large-brained precocial mammals exhibit a reduced fertility rate by producing much larger offspring after longer interbirth intervals (Isler and van Schaik 2009*a*). This is probably because relatively large-brained immatures are highly vulnerable to temporary shortfalls in energy supply (the "brain mal-

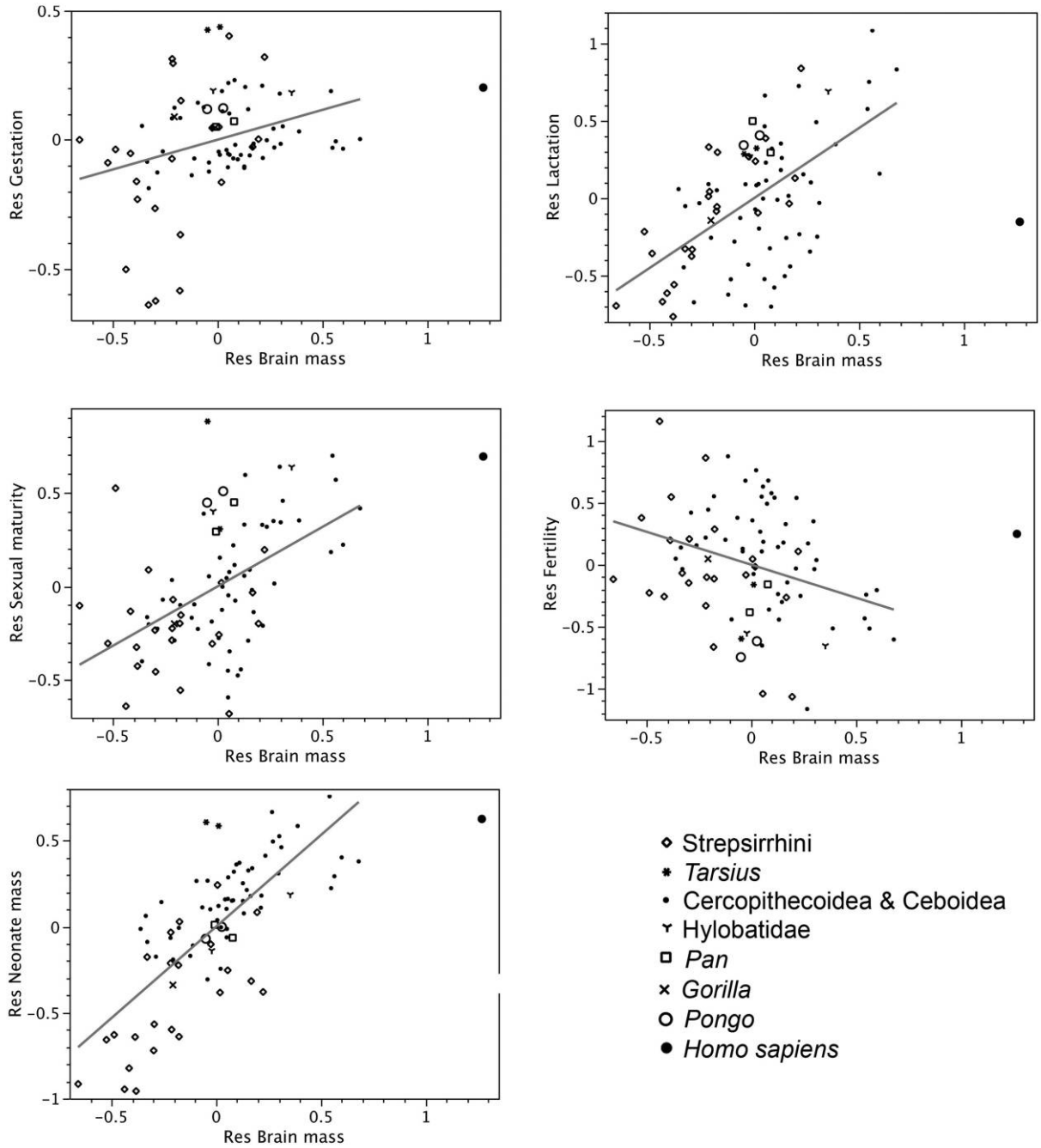

Figure 2. Residuals of life history traits versus residuals of endocranial volume in primates ($N = 86$ species; *Homo sapiens* was excluded while calculating the regressions). Residuals were obtained from least squares regressions of the respective trait versus female body mass. A color version of this figure is available in the online edition of *Current Anthropology*.

Table 2. Life history parameters of humans and other great apes

Parameter	*Gorilla gorilla*	*Pan troglodytes*	*Pan paniscus*	*Pongo pygmaeus*	*Pongo abelii*	Human mean 14
Female body mass (kg)	71.5	40.4	33.2	36.9	41.1	45.26
Female brain size (cm^3)	434	357	326	337	346	1,213
Gestation length (m)	8.45	7.73	7.6	8.22	8	8.9
Neonate body mass (g)	2,124	1,846	1,447	1,968	1,969	3,319
Twinning rate	1/100	2.8/100	?	?	?	1/100
Interbirth interval (years)	5	5.43	4.8	7.35	9.3	3.331
Weaning age (years)	3.5	4	3	5.3	5.5?	2.83
Female age at first reproduction (years)	10.2	13.25	14.2	15.7	15.4	18.84
Maximum life span	55	59.4	54.5	56.3	59	85

Sources. Values are taken from van Schaik and Isler (2012), from Ely et al. (2006) for chimpanzee twinning rate, from Walker et al. (2006) for the mean of 14 human subsistence populations, and from Barrickman et al. (2008) for human brain size.

nutrition risk" hypothesis of Deaner, Barton, and van Schaik 2003), so that a relatively large neonatal body mass is needed to buffer this risk. In addition to larger newborns, the reduced allocation to production slows down development and delays the age at first reproduction in relatively large-brained precocial mammals and especially in primates (table 1). Indeed, a recent analysis for a carefully compiled data set of wild primates showed that brain size is the best predictor of the duration of all stages of developmental life history except the (poorly delineated) lactational period and that taking body size into account does not improve the fit (Barrickman et al. 2008).

To assess to what extent this effect of brain size on life history also characterizes humans, we should look at human life history traits in relation to relative brain size. Although some have questioned whether extant human foragers represent the "natural" condition for our species, they are certainly situated at the lower end of the spectrum of human reproductive capacity and can thus serve as a conservative estimate for comparison with extant ape species.

If we plot life history traits versus relative brain size in nonhuman primates (fig. 2) and assess the values of human foragers and horticulturalists based on those expected for other primates, the main human characteristic is a distinctly shortened period to weaning, and thus an increased annual fertility rate, for its brain size. On the other hand, humans exhibit considerably smaller neonates but only a slight decrease in gestation length and a perfectly normal age at first reproduction for their brain size.

Thus, the main deviation from expectation is that humans manage to have much higher investment in reproduction (both pre- and postnatally) than expected for their brain and body size. The same conclusion is reached when we compare the life history of human foragers directly with that of extant nonhuman hominoids (table 2). This difference points to major changes in lifestyles adopted by hominins, which will be explored after we determine that a given lineage has a maximum brain size it can achieve.

Brain Size and Maximum Population Growth Rates

In large-brained mammals and primates, the developmental slowdown and reduced reproductive rate are accompanied by an increased adult life span (Isler and van Schaik 2009*a*), but the question arises whether the increased life span can con-

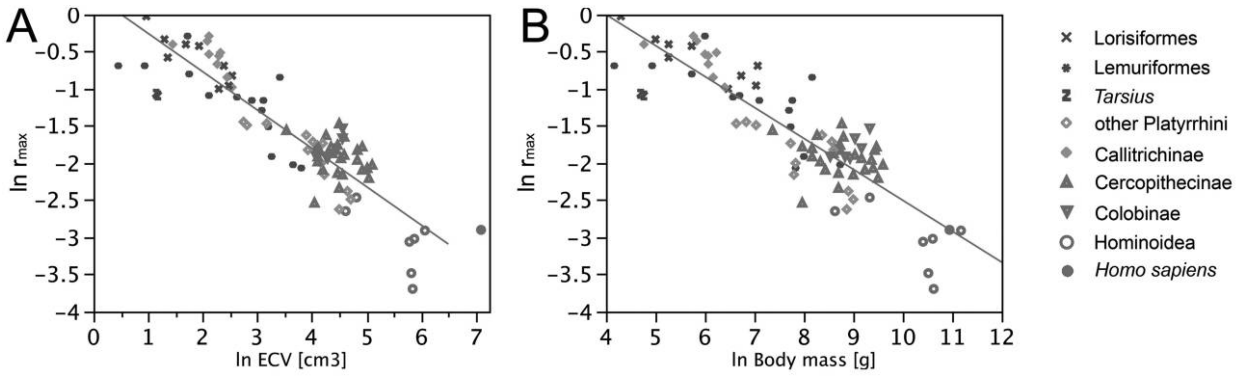

Figure 3. Maximum population growth rate r_{max} as a function of (*A*) endocranial volume (ECV) and (*B*) body mass in nonhuman primates ($N = 85$ species; *Homo* is shown for comparison but is not included in the calculation). A color version of this figure is available in the online edition of *Current Anthropology*.

Table 3. Maximum population growth rates of humans and other great apes

Rate	*Gorilla gorilla*	*Pan troglodytes*	*Pan paniscus*	*Pongo pygmaeus*	*Pongo abelii*	Human mean 14
Interbirth interval (years)	5	5.43	4.8	7.35	9.3	3.331
Female age at first reproduction (years)	10.2	13.25	14.2	15.7	15.4	18.84
Maximum life span	55	59.4	54.5	56.3	59	85
r_{max}	.054	.049	.047	.031	.025	*
DT_{min} (years)	12.8	14.1	14.7	22.4	27.7	*
Maximum age at last birth	45?	45	45	45?	45	47
r_{max}** (using maximum age at last birth)	.051	.044	.043	.025	.017	.047
DT_{min}** (years)	13.6	15.8	16.1	27.7	40.8	14.7

Sources. Maximum age at last birth for apes (Emery Thompson et al. 2007; Wich et al. 2004); for humans (Hill and Hurtado 1996; Howell 1979).
Note. The human r_{max} and DT_{min} values calculated from maximum life span would be artificially high (*). Because of midlife menopause in humans, r_{max} and DT_{min} are more realistically calculated using maximum age at last reproduction instead of maximum life span (**). Then, however, the same rationale must be followed for the other apes. These values should not be compared with those of other primates or mammals. DT_{min} = minimum time to double population size.

tinue to fully compensate the reduced production per unit time as brain size increases. On average, females of every species leave roughly two viable adult offspring per lifetime, but species vary dramatically in their maximum reproductive capacity under ideal conditions. We need a measure of reproductive capacity that represents maximum possible lifetime reproductive success. The net reproductive rate ($R_{(0)}$) of extant populations is derived from life tables and will hardly ever represent optimal conditions. A far better estimate of maximum reproductive capacity is maximum population growth rate (r_{max}). Additionally, in contrast to a rough product of average fertility and maximum fertile life span, r_{max} takes generation time into account. To give a stark example, if two otherwise identical species differed because in one, females start to reproduce at age 1 and die at age 21, whereas in the other, females start to breed at age 21 and die at age 41, the first species would soon outcompete the second (Lewontin 1978). The value of r_{max} is defined as

$$1 = e^{-r} + be^{-ra} - be^{-r(w+1)},$$

where a = age at first reproduction, w = age at last reproduction, or maximum life span, and b = birth rate (of female offspring) per year (Cole 1954). We can calculate r_{max} from age at first reproduction, maximum life span, and annual fertility rates by solving Cole's (1954) equation numerically (Ross 1988, 1992). Enough reliable data for its calculation exist for many extant primate species. From r_{max}, the minimum number of years needed to double population size (DT_{min}) is calculated as

$$DT_{min} = \frac{\ln(2)}{r_{max}}.$$

We have shown previously (Isler and van Schaik 2009*b*) that this r_{max} shows a very strong negative correlation with brain mass in mammals and precocial birds, and indeed, that brain mass is a better predictor of r_{max} than is body mass. The same is found within primates as a group (fig. 3) and if we control for phylogenetic nonindependence (table 1). This finding is not a statistical artifact because brain mass might be a better estimate of body size than body mass itself by being less prone to error variance (Economos 1980) and because the relationship is found only for brain mass and not for the mass of other organs, which also show a low degree of variation (see Isler and van Schaik 2009*b*, app.). What is especially striking is that great apes, in particular orangutans, show the lowest possible r_{max}, quite possibly close to what is minimally viable demographically.

Similarly, although r_{max} is based on an average annual fertility rate, we may expect that using a maximum fertility rate would only strengthen the observed relationship, as small-brained species probably exhibit a higher plasticity of reproduction in response to ecological conditions. In this case, r_{max} would underestimate the maximum reproductive capacity mostly in small-brained species, yielding an even stronger negative correlation between maximum reproductive capacity and brain size. Using r_{max} is therefore a conservative approach for our purpose.

The Gray Ceiling in Primates

The negative relationship between r_{max} and brain mass, controlling for body mass, indicates that as brain size increases, the increase in life span is increasingly unable to fully compensate for the costs incurred by long developmental periods

Table 4. Multiple regression of variables affecting r_{max} simultaneously in nonhuman primates ($N = 85$ species, $r^2 = 0.869$)

Variable	Estimate	*t* ratio	*P*
Intercept	.083	.22	.829
ln female endocranial volume	−.663	−5.24	<.0001
ln female body mass	.067	.69	.495
Terrestriality	.168	3.91	.0002
Nocturnality	−.131	−2.40	.019
Hominoidea vs. others	−.232	−3.53	.0007

Note. Parametrization of the covariates was chosen empirically in order to explain as much variation of r_{max} as possible as follows: terrestriality and nocturnality were coded as binary variables (none or <5% vs. >5% of terrestriality; nocturnal vs. diurnal or cathemeral).

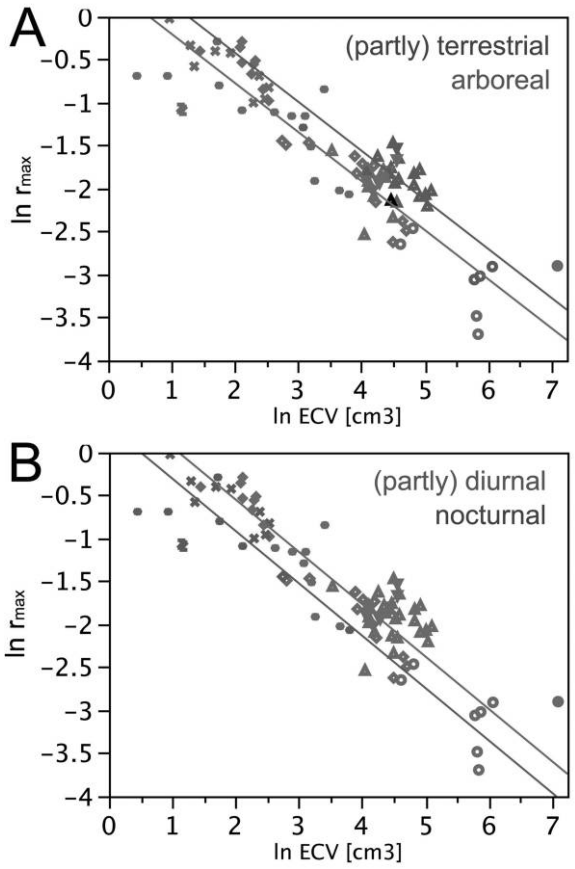

Figure 4. Relationship between maximum population growth rate r_{max} versus endocranial volume (ECV) in nonhuman primates as affected by (*A*) terrestriality and (*B*) nocturnality. To illustrate the magnitude of differences, slopes of the regression lines were forced to be identical in both groups. Symbols as in figure 3; multivariate statistics in table 5. A color version of this figure is available in the online edition of *Current Anthropology*.

and lower reproductive rates. The most likely reason is that there is a realistic minimum mortality rate set by freak accidents and freak environmental events (droughts, floods, fires, epidemics, lightning strikes, etc.) that are truly unavoidable regardless of niche or behavior. Thus, as this minimum mortality level is approached, further increases in brain size will of course continue to yield lower production but will inevitably lead to only a modest improvement in survival and thus maximum life span. As a result, r_{max} declines.

It is likely that such a low reproductive potential as found in great apes compromises demographic viability for two reasons. First, where survival must be near perfect just to maintain population stability, there is virtually no room for selective mortality. This means that drastic changes in the environment must be met with phenotypically plastic responses (including individual learning and innovativeness and socially learned innovations, i.e., culture) rather than selective mortality and that populations are almost certainly at higher risk of local extinction in such conditions. Indeed, a population's maximum reproductive capacity directly affects the maximum rate of environmental change that it can adapt to without going extinct (Lynch and Lande 1993). Second, low reproductive potential even under perfect conditions also implies a limited ability of a species to recover from population crashes and thus a species that is less likely to build up enough individuals to colonize new areas or habitats until the next crisis period. We can therefore use this reproductive potential as an estimate of the ability to stave off population or species extinction.

A major consequence of this rule is that ever-lower r_{max} with increasing brain size should lead us to expect a particular maximum brain size, which we call the gray ceiling. As brains exceed this size, population extinction becomes increasingly likely, leading eventually to the extinction of the population or species whenever major changes in habitat (e.g., due to climate change) take place. Given that among primates, great apes are at the minimum of demographic viability, we must conclude that in this lineage no major increase in brain size should be possible. Nonetheless, humans, of course, achieved exactly this, raising the question how this was possible.

Calculating r_{max} of extant humans is complicated by the existence of midlife menopause, which is unique among primates. If instead of maximum life span we use maximum observed age at last reproduction (for females) and do the same thing for great apes, the r_{max} of humans lies between the values of gorillas and chimpanzees (table 3) instead of far lower, as one would expect based on the brain-size effect on r_{max}. Notice that Sumatran orangutans have a potential DT_{min} of over 25 years, which may well be the lowest value observed for all extant mammals (the actual value itself is not to be taken too seriously because it refers to a theoretical construct; it is only meant to be used for comparative purposes). In the more seasonal African environments, such a value may not be realistic, and the observed values of the African great apes (between 13.6 and 16.1 years) suggest a realistic value of the potential DT_{min} of around 20 years.

Predicting Human r_{max}

In comparison with other hominoids, humans exhibit a much larger r_{max} than expected for our extremely large brain size (fig. 3*A*). But what value of r_{max} would be predicted for a typical hominoid of humanlike brain and body mass? To answer this question, we must consider possible correlates of either brain size or r_{max} to construct a multivariate linear model that explains as much variation in primate r_{max} as possible.

In a multivariate analysis within nonhuman primates ($N = 85$ species; table 4), r_{max} is affected by arboreality (species that are at least partly terrestrial have a higher r_{max}; fig. 4*A*) and by nocturnality (nocturnal species have a lower r_{max} than diurnal or cathemeral species; fig. 4*B*) but not by diet (percentage of leaves or fruit or animal matter in the diet).

Table 5. Hypothetical life history traits of *Homo sapiens* predicted from primate and hominoid trends

Trait	Model A: primate	Model B: hominoid	Actual values: mean 14
Litter size	<1	<1	1.011
Neonate mass (g)	7,377	6,865	3,319
Gestation length (months)	10.2	10.9	8.9
Lactation length (years)	5.46	7.57	2.83
Interbirth interval (years)	5.89	7.89	3.33
Age at first reproduction (years)	17.3	22.6	18.8
Maximum life span (years)	68.7	79.1	85
r_{max}	.027	.022	.047
DT_{min} (years)	25.4	32.3	14.5

Source. For comparison, the actual mean values of 14 extant human populations are taken from Walker et al. (2006).
Note. Model A includes terrestriality, nocturnality, and female endocranial volume and body mass, whereas model B additionally takes membership to Hominoidea into account. Using the predicted values for interbirth interval and age at first reproduction and setting litter size to 1 and maximum age at last reproduction to 47 years, r_{max} values for *Homo sapiens* can also be calculated directly, yielding .031 (model A) and .014 (model B).

But even if these covariates are controlled for, hominoid species exhibit a lower r_{max} than other primates ($P = .0007$ in a multiple regression; table 4).

If humans followed the general primate trend, their r_{max} would be estimated as 0.027 (predicted from a multivariate model including terrestriality, nocturnality, and female body mass and endocranial volume [ECV]; table 5). If we take into consideration that we are hominoids too, the predicted r_{max} would be even lower, about 0.022. This means that the DT_{min} under optimum conditions would be around 30 years, which would almost certainly not lead to demographically viable populations under the unstable African conditions in which humans evolved.

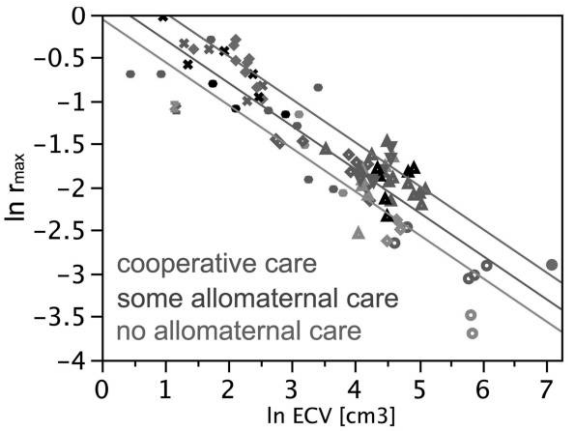

Figure 5. Maximum population growth rate r_{max} versus brain size (endocranial volume [ECV]) in nonhuman primates for species that exhibit cooperative breeding (*Homo sapiens* is excluded from the calculation); species that show at least some amount of allomaternal care such as paternal care, communal nursing, or babysitting; and species that show no allomaternal care at all. To illustrate the magnitude of differences, slopes of the regression lines were forced to be identical in the three groups. Symbols as in figure 3; multivariate statistics are given in table 7. A color version of this figure is available in the online edition of *Current Anthropology*.

These hypothetical human r_{max} values, assuming a lifestyle like that of other primates, are lower than those found for any extant mammalian species. The lowest observed r_{max} values are found in species that experience very low adult mortality rates (i.e., live in extremely stable habitats and hardly suffer from predation), such as orangutans: 0.025 (*Pongo abelii*) and 0.031 (*Pongo pygmaeus*); killer whales: 0.028 (*Pseudorca crassidens*) and 0.046 (*Orcinus orca*); chimpanzees: 0.049 (*Pan troglodytes*) and 0.047 (*Pan paniscus*); gorillas and African elephants: 0.054; and dugongs: 0.058. In conclusion, regardless of which model we use, a species with human brain and body mass would not be able to survive if it otherwise adheres to a primate or hominoid lifestyle let alone whether it was not completely arboreal and living in African woodland or savanna.

Why Could Humans Break through the Gray Ceiling?

Up to this point, we have shown that a human brain–body size relationship would not be demographically feasible in a primate following a typical hominoid lifestyle even if we take differences in diet and locomotor patterns into account. The main distinction affecting interbirth intervals and weaning age is our system of cooperative care for infants and mothers (Burkart, Hrdy, and van Schaik 2009; Burkart and van Schaik 2010; Hrdy 2005). Callitrichids are the only other primates that exhibit cooperative breeding to a similar extent. Indeed, the maximum reproductive rate of callitrichines is, because of twinning, on roughly the same grade as *Homo sapiens* (fig. 5).

A multivariate regression yields a clear additional effect of this very rough measure of the extent of allomaternal care in nonhuman primates taking into account the known covariates such as terrestriality, nocturnality, and diet (table 6). A more quantitative measurement of the extent and dimensions of

Table 6. Multiple regression of variables affecting r_{max} simultaneously in nonhuman primates including a rough measure of allomaternal care ($N = 72$ species, $r^2 = 0.897$)

Variable	Estimate	*t* ratio	*P*
Intercept	−.580	−1.39	.168
ln female endocranial volume	−.540	−4.32	<.0001
ln female body mass	.100	1.01	.317
Terrestriality	.106	2.40	.019
Nocturnality	−.001	−.01	.989
Hominoidea vs. others	−.316	−4.86	<.0001
Cooperative breeding:			
Cooperative vs. some allomaternal care	.385	4.07	.0001
Some vs. no allomaternal care	.301	4.41	<.0001

Note. Allomaternal care was assigned to three categories: "cooperative care": cooperatively breeding species (callitrichines); "some allomaternal care": species in which at least a modest amount of help for the mother is provided through paternal care, babysitting, allonursing, or passive food sharing; "no allomaternal care": the remaining species. For the other covariates, see table 4. If the variable "Hominoidea vs. others" is excluded, the effect of allomaternal care on r_{max} is still significant. In comparison to the model in table 4, nocturnality does not affect r_{max} in this model. This indicates that the difference in r_{max} between nocturnal and diurnal primates is better explained by the differences in the breeding system than by their activity pattern.

allomaternal help confirms this relationship (van Schaik and Isler 2012).

The inclusion of allomaternal care in the model to predict hypothetical human life history traits yields values that are much closer to the actual values of extant human subsistence populations (table 7). It is not clear a priori which of the two models (general primate [C] or hominoid [D] in table 7) provides the most accurate answer.

Southeast Asian hominoids (gibbons, orangutans) live in regions that were at least in part affected less by the series of Pleistocene glaciations than Africa (Whitmore 1984). This relative stability may have allowed for slower viable r_{max} (perhaps in part achieved through lower BMRs; Pontzer et al. 2010), and they may pull the estimates for humans down. On the other hand, the heavily terrestrial gorillas may bias the estimates in the opposite direction, and the chimpanzee values are actually predicted quite well by the hominoid model. For now, therefore, we present both sets of results and expect that the true values may be intermediate.

Table 7 shows that the predicted age at first reproduction, fertility rates, interbirth intervals, and r_{max} are fairly accurate in both models. Note that in both models C and D, interbirth intervals are anomalously shorter than lactation periods, which is due to the result that in nonhuman primates, allomaternal care reduces interbirth intervals more than it shortens lactation periods. We are thus confident that cooperative care is indeed responsible for the observed differences between human and ape life history traits. This interpretation is supported by another result in table 7. Human life span is somewhat longer than predicted, which may be linked to our tendency to support the sick and injured, which should improve survival relative to the baseline situation of no support, as in great apes, and thus over time maximum life span.

There is one major discrepancy between model and observation that may therefore reflect another effect than cooperative breeding. Neonate mass is much smaller and gestation length somewhat shorter than the very large values predicted (largely due to our very large brain size). This discrepancy may be linked to the obstetrical dilemma, caused by the narrowing of the pelvic canal as a result of bipedalism (Montagu 1961; Trevathan 1987; Washburn 1960), which at some point has become limiting for the size of the human neonate. It is certainly consistent with the secondary altriciality of human neonates. Note, however, that a more altricial state at birth can explain only this one minor difference between the life histories of humans and great apes, whereas the overall difference can be attributed to the extensive allomaternal care in humans.

Table 7. Hypothetical life history traits of *Homo sapiens* predicted from a primate trend including cooperative breeding

Trait	Model C: primate and help	Model D: hominoid and help	Actual values: mean 14
Litter size	<1	1.036	1.011
Neonate mass (g)	6,824	6,476	3,319
Gestation length (months)	11.1	11.8	8.9
Lactation length (years)	3.78	5.28	2.83
Interbirth interval (years)	3.16	4.41	3.33
Age at first reproduction (years)	16.6	20.9	18.8
Maximum life span (years)	67.5	76.7	85
r_{max}	.057	.042	.047
DT_{min} (years)	12.2	16.5	14.5

Source. For comparison, the actual mean values of 14 extant human populations are taken from Walker et al. (2006).
Note. Model C includes female brain and body mass, terrestriality, and the allomaternal care category, whereas model D additionally takes membership to Hominoidea into account. Using the predicted values for litter size, interbirth interval, age at first reproduction, and maximum age at last reproduction set to 47 years, r_{max} values for *Homo sapiens* can also be calculated directly, yielding .054 (model C) and .035 (model D).

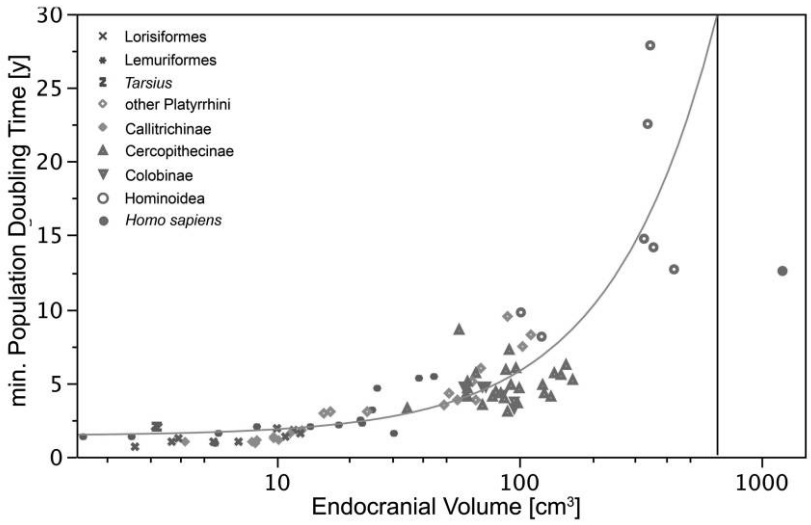

Figure 6. Minimum population doubling time versus endocranial volume (ECV) in nonhuman primates (*Homo sapiens* is excluded from the calculation). The vertical line represents an ECV of 655 cm^3. Note that values are not log transformed here. A color version of this figure is available in the online edition of *Current Anthropology*.

When Did Humans Break through the Gray Ceiling?

In this section, we aim to predict maximum potential population growth rates of extinct hominins from the primate model to find out when they would have reached the region of demographic nonviability without a change in the breeding system. In a first attempt, we plot DT_{min} of nonhuman primates versus their ECVs (fig. 6). To get a reasonable estimate of a threshold value, we conservatively assume that a doubling time beyond 30 years ($r_{max} = 0.023$) would not yield viable populations. This is a very conservative estimate, as no other living mammal exhibits such a low maximum reproductive rate. From the relationship between DT_{min} and ECV, we conclude that this value would be reached with an ECV of about 650 cm^3. If terrestriality is included in the model, which is rather likely for all early hominins (remember we do not require a high percentage of terrestrial locomotion here), the threshold would be even lower, about 610 cm^3. This crude first attempt suggests that the first species to break through the gray ceiling was early *Homo*, which must therefore have had extensive allomaternal care. Using the more sophisticated model D—which was specific for the hominoids and included not only brain size but also body mass, terrestriality, and the level of allomaternal care—the effect of a change in breeding system can be specified in greater detail.

Table 8 lists predicted interbirth intervals and the corresponding DT_{min} for fossil hominin taxa groups. If we assume no allomaternal help, the predicted age at first reproduction (AFR) ranges from 12.6 years in *Australopithecus afarensis* to 26.1 years in the very large-brained Qafzeh *Homo sapiens*, and the predicted interbirth interval (IBI) is from 6 to 8.4 years (table 8). If we assume cooperative breeding, the predicted AFR is between 10.9 and 22.6 years, while the predicted IBI is 3.4 for *A. afarensis* and 4.7 for Qafzeh *H. sapiens*. Estimating twinning rate from our models is not feasible because the twinning callitrichines introduce a strong body-mass dependency of twinning rates. To estimate population growth rates, we therefore set litter size to 1.01; that is, twinning occurs in 1% of births. The results of the model are illustrated in figure 7.

We assume that a DT_{min} of somewhere between 15 years (extant chimpanzees) and 20 years would still be feasible. It is apparent that no help for mothers (as in orangutans) results in a very steep relationship between population doubling times and brain size. Species are included in the category of "some help" even if they exhibit minimal helping behaviors, such as passive food sharing or babysitting, with only minimal frequency. Extant African apes (gorillas and chimpanzees) are at this lower end of the spectrum. From our model, it seems that an ECV of more than 700 cm^3 would not yield sustainable populations with such an intermediate system of allomaternal care. Only with full cooperative breeding (as in extant humans or callitrichines) would fossil hominins have been able to provide sufficient energy for a sustainable population growth rate and support a brain that is larger than 700 cm^3.

In conclusion, a gradual change in lifestyle toward a substantial increase in allomaternal help (including provisioning of mothers and weaned offspring) may have evolved early in, or even before, the genus *Homo*. (For the challenge of allocating the earliest *Homo* fossils to meaningful clusters, see Antón 2012.)

Were Early *Homo* Cooperative Breeders?

We believe that *Homo erectus* (= *ergaster*), as it emerged at around 1.8 Ma, was a good candidate for having extensive allomaternal care for two major reasons. First, they were likely the first systematic hunters of large game (Foley and Lee 1991; Pobiner et al. 2008). Large-game hunting requires cooperation during the hunt, cooperative defense against other dangerous carnivores, extremely high tolerance around kills, and frequent food sharing, perhaps even to the point of provisioning. These features are all more likely among cooperative breeders (van Schaik and Burkart 2010). Indeed, among mammals, carnivores are more likely to be cooperative breeders (Smith et al. 2012; Solomon and French 1997; Spencer-Booth 1970).

Second, the weaned juveniles were less likely to make a living on their own and would have strongly benefited from allomaternal support. They lived on the savanna, where resources harvested as efficiently by juveniles as adults, such as soft fruits, are much scarcer than in forests (Hawkes et al. 1998), leading to reduced juvenile foraging efficiency. The latter is especially likely if they had already acquired a great reliance on meat

Table 8. Predicted life history and demographic parameters of early hominins

				Allomaternal care during predicted interbirth interval (years)			Allomaternal care during predicted DT_{min} (years)		
Species and sample	Time (Ma)	Female endocranial volume	Female body mass	No	Some	CB	No	Some	CB
Australopithecus afarensis:									
A.L. 333-105	3.2	343	29.3	6.04	4.59	3.43	**17.7**	**14.0**	**10.3**
A.L. 444-2	3.2	550	51.3*	6.88	5.24	3.91	23.4	**17.7**	**12.6**
Australopithecus africanus:									
STS 71	2.75	428	26.6	6.21	4.73	3.53	20.1	**15.6**	**11.4**
STW 505	2.5	560	46.8	6.85	5.21	3.89	23.8	**18.0**	**12.7**
Australopithecus boisei:									
KNM-ER 732 female	1.7	500	32.0	6.48	4.93	3.68	22.1	**17.0**	**12.2**
OH 5 male	1.8	530	57.6	6.91	5.26	3.93	22.8	**17.3**	**12.4**
Early *Homo*:									
KNM-ER 1813	1.89	509	34.9	6.56	4.99	3.72	22.4	**17.1**	**12.3**
KNM-ER 1805	1.89	580	30.3*	6.61	5.03	3.76	24.6	**18.6**	**13.1**
KNM-ER 1470	1.89	752	45.6	7.18	5.46	4.07	30.0	21.8	**14.8**
Homo erectus:									
Africa:									
KNM-ER 42700 (Ileret)	1.55	690	45*	7.06	5.38	4.01	27.9	20.5	**14.2**
KNM-ER 3733	1.8	850	59.2	7.50	5.71	4.26	33.4	23.7	**15.7**
Georgia:									
D3444	1.77	638	47*	7.00	5.33	3.97	26.2	**19.5**	**13.6**
D2280	1.77	775	52.6*	7.31	5.56	4.15	30.7	22.2	**15.0**
Asia:									
Zhoukoudian XI female	.42	1,015	51.8	7.64	5.81	4.34	41.2	27.9	**17.6**
Zhoukoudian X male	.42	1,225	65.6*	8.06	6.13	4.57	53.2	33.3	**19.8**
Archaic *Homo sapiens*:									
Steinheim	.25	1,110	60.5	7.86	5.98	4.47	45.9	30.1	**18.6**
Jebel Irhoud	.09	1,305	80.5	8.3	6.31	4.71	58.0	35.2	20.5
Homo neanderthalensis:									
Saccopastore female	.12	1,245	66.6	8.09	6.16	4.59	54.6	33.9	20.0
Le Moustier male	.041	1,565	81.2	8.56	6.52	4.86	89.3	45.8	23.8
H. sapiens:									
Zhoukoudian 102 female	.015	1,380	43.2	7.91	6.02	4.49	74.5	41.7	22.5
Qafzeh 9 female	.1	1,531	64.6	8.35	6.36	4.74	89.5	46.1	23.8
Extant females	0	1,213	45.3	7.79	5.93	4.42	55.1	34.3	20.1

Sources. Endocranial volumes (cm^3) and body mass (kg) estimates of fossils are taken from Gabunia et al. (2000), Kappelman (1996), Spocter and Manger (2007), Spoor et al. (2007), and Ruff (2010).

Note. As sex determination is notoriously difficult for early hominins, we list both a small and a large morph from reasonably complete crania. Body mass estimates denoted with an asterisk do not correspond to the same fossil as the endocranial volume. The body mass for a small African *H. erectus* (45 kg) is very roughly estimated from comparing other estimates with the size of the Ileret cranium. Interbirth intervals and age at first reproduction are estimated using model D from table 6 (excluding the effect of nocturnality). For calculating minimum population doubling time (DT_{min}), maximum age of reproduction is set to 47 years and twinning rate to 1/100. Values <20 years are highlighted in boldface. CB = cooperative breeding. The predictions for 1.9 Ma *Australopithecus sediba* would be very similar to *A. africanus* min. (endocranial volume of 420 cm^3 in a juvenile male, body mass of the adult female estimated at 27 kg; Berger et al. 2010).

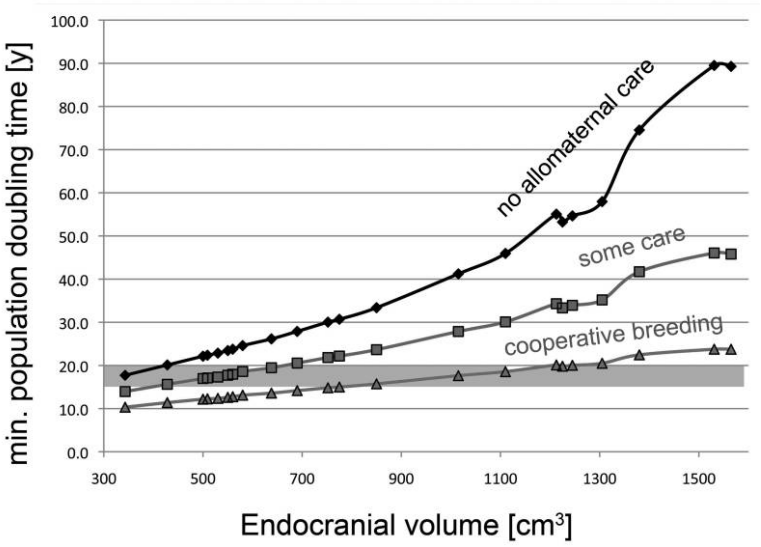

Figure 7. Minimum population doubling time (DT_{min}; years) of fossil hominins predicted from model D (individual values listed in table 8). We assume that a DT_{min} of somewhere between 15 years (extant chimpanzees) and 20 years would still be feasible (shaded bar). The lack of smoothness results from the inclusion of body mass in the model. A color version of this figure is available in the online edition of *Current Anthropology*.

(Domínguez-Rodrigo and Pickering 2003), because the difficulty of learning how to hunt means that provisioning meat has strong positive effects on the fitness prospects of the young. More seasonal habitats are more likely to contain cooperative breeders (Hatchwell 2007; Rubenstein and Lovette 2007). The argument is further supported by *H. erectus* (= *ergaster*) occupying a much larger geographic range than earlier hominin species. Hrdy (2005, 2009) has argued convincingly that colonizing hostile new habitats is facilitated by cooperative breeding.

Identifying the source of extensive allomaternal care in early *Homo* is difficult, as the defining feature of human caretaking seems to be its large flexibility (Hrdy 2009). In present-day human societies, grandmothers and males, but also not directly related adults (Hill and Hurtado 2009), play a major role. As midlife menopause is extremely rare in mammals (Packer, Tatar, and Collins 1998), we cannot apply comparative evidence to the evolution of grandmothering. However, males were almost certainly involved in meat sharing and thus allomaternal care as soon as confrontational scavenging or hunting of large game was present (Marlowe 2007). In sum, while the brain size of *H. erectus* and various other indicators suggest that females of this species received much allomaternal care, we assume that male-female pair bonds accompanied by selective food sharing were sources of this care, but we can make no conclusions about the role of grandmothers.

Discussion

The analyses reported here suggest that the inability of survival to keep up with reduced production as brain size increases leads to a reduction in r_{max} in larger-brained organisms. There comes a point where no further increases in brain size are possible because the long-term viability of populations is severely compromised. This point we call the "gray ceiling." For great apes living a great-ape lifestyle, we put this conservatively at 600–700 cm^3. This explains why extant great apes and extinct australopithecines seem to have converged on similar brain sizes, but it makes the "escape" from great-ape level brain sizes by *Homo* even more striking. Assigning a distinct boundary to a highly fragmentary fossil record is tricky, but *Homo rudolfensis* (i.e., KNM-ER 1470) is a likely candidate for such a change in lifestyle. The first well-documented hominin to show brains that exceed this size was *Homo erectus* (= *ergaster*), which arose in Africa at around 1.8 Ma, occupied savanna habitats, hunted large game, and rather quickly had moved into other geographic regions.

Allomaternal care tends to lead to higher female reproductive output in both primates (Mitani and Watts 1997; Ross and MacLarnon 2000) and carnivores (Isler and van Schaik 2009*a*). We propose that as in other mammals and birds, the adoption of cooperative breeding (Hrdy 2005, 2009) had allowed *H. erectus* (= *ergaster*) to increase its r_{max}, which, given its value near the gray ceiling, made possible an expansion of its brain size. As a conservative estimate, our gray ceiling value of 600–700 cm^3 provides an upper boundary to brain size if a species is adhering to an apelike lifestyle. Of course, we cannot exclude the possibility that cooperative breeding predated a pronounced increase of encephalization by several million years, as suggested in Lovejoy's (2009) scenario for

the adaptive suite of characters assigned to *Ardipithecus ramidus*. In this case, however, another explanation would be needed for the long time lag between the onset of provisioning and increase in brain size. Australopithecines were adept bipeds without sectorial canine complexes, but there is no evidence for a shift in life history traits and developmental trajectories before *Homo* (Dean 2006; Dean and Lucas 2009; Schwartz 2012; but see DeSilva 2011).

In conclusion, if we rely on estimating the effect of evolutionary processes known to operate in primates or in vertebrates in general, there is evidence for several factors that allowed for brain-size expansion throughout the evolutionary history of the human lineage. A more seasonal environment, a change in diet toward higher-quality food sources, and more efficient locomotion all may have played a role (Potts 2011). Instead of a comprehensive but unique "adaptive suite" of human traits (Lovejoy 2009), however, we find broad comparative support for a decisive role of cooperative breeding as the initial trigger of many subsequent changes in human biology (Burkart, Hrdy, and van Schaik 2009; Burkart and van Schaik 2010). As such a redistribution of energy toward mothers and infants is possible without changing the overall energy budget, it may have facilitated subsequent changes that led to the relatively high energetic throughput of modern humans as compared with extant apes (Pontzer 2012; Pontzer et al. 2010).

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